Water availability and species identity control shrub colonization in abandoned semiarid steppes[1]

Short title: Patch dynamics in drylands

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Abstract

The increase in shrub cover and density is a widespread phenomenon in drylands worldwide. Its causes and consequences are complex and strongly idiosyncratic. Detailed knowledge of the rate of shrub colonization, and its abiotic and biotic drivers is crucial to fully understand and manage these areas. We used a set of aerial photographs (1956, 1978, 1985, 1998 and 2009) and field data to relate shrub patch dynamics, and abiotic and biotic properties of 27 abandoned steppes in SE Iberian Peninsula. Shrub patch density in 2009 ranged from 11 to 143 patches ha^{-1}, and increased by an average of ~ 180% between 1956 and 2009. Temporal changes in shrub patch density followed non-linear functions (monomolecular, logistic and exponential) describing early, gradual and late recruitment, respectively. Differences in shrub patch colonization rate were related to the identity of patch-forming species, but contingent on water availability. Total increases in shrub patch density were larger when patches were dominated by late colonizer species. Overall shrub patch dynamics was mostly related to the identity of patch-forming species and climatic conditions, and to a lesser extent physical factors such as aspect and rock cover. Given the sensitivity of patch-forming species to climatic conditions, new challenges for steppe management will emerge over the next decades. Species able to thrive under harsh conditions may increase their dominance at the expense of species adapted to less demanding conditions.

Keywords: Shrub encroachment, long-term plant dynamics, aerial photography, standardize precipitation index, drylands, *Stipa tenacissima*

1. Introduction

The proliferation of woody species is a common phenomenon in drylands worldwide (van Auken, 2009). Information derived from time series of aerial photographs has advanced our knowledge of the dynamics and extent of shrub encroachment (Briggs et al., 2002; Peters et al., 2006). However, research on the drivers of shrub colonization has mostly focused on the effect of physical factors, particularly soil properties and topographic features such as aspect and elevation (Browning et al., 2008; Davies et al., 2010; Levick and Rogers, 2011) or grazing (Bartolomé et al., 2005; Roques et al., 2001; Ward et al., 2014). In contrast, the identity of the colonizing shrub species as major driver of shrub expansion has seldom been studied. This is despite the strong relationship between climate, morphological/-functional traits and shrub dynamics (Eldridge et al., 2011; Pueyo et al., 2010).

Different shrub assemblages, which are the result of long-term processes such as habitat filtering and niche differentiation (Gross et al., 2013), may exhibit contrasting colonization dynamics. Differences in life-history traits among species (e.g. age at maturity or number of offsprings) may generate different sequences of shrub colonization (e.g. Iannone et al., 2014). Different sequences may also result from contrasting survival strategies among co-occurring shrub species to disturbances such as fire (e.g. Hodgkinson, 1998). However, most studies addressing the drivers of shrub cover change in drylands consider the encroaching vegetation as a single functional group (e.g. D'Odorico et al., 2012), overlooking potential species-specific effects of shrubs on colonization dynamics.

Variable colonization dynamics can also result from changes in climatic conditions, such as water availability during the colonization process (Browning et al., 2008). Thus, coupling species-level information on colonization with data on past climatic events may provide further insights into the linkages between climate and vegetation and, therefore, on the mechanism behind shrub colonization (Munson et al., 2015). This is especially relevant for dryland environments where climate projections predict increased variability in precipitation as well as

increased frequency of extreme events, such as drought (IPCC, 2007). Clarifying how drought intensity mediates species-specific effects of shrub colonization can be of great help to predict future trends in shrub population dynamics, and assess the consequences of future global change regimes on the provision of ecosystem services (Ruppert et al., 2015).

Knowledge of the drivers of shrub colonization is of major importance in those ecosystems where planting woody species has become a major priority in restoration programs (Cortina et al., 2011; Maestre et al., 2001; Padilla et al., 2009b). For instance, open steppes dominated by *Stipa tenacissima* L. are conspicuously distributed in the semiarid regions of the western Mediterranean basin. For centuries, the provision of *S. tenacissima* fiber was the main management priority in these steppes. Large shrubs were removed to favor *S. tenacissima* production (Maestre et al., 2007). Over the last decades, an increase in shrub cover has been reported in southern European steppes, probably as a result of the abandonment of traditional agricultural practices (Alados et al., 2004; Maestre et al., 2007) and linked to desertification reversal (Maestre et al., 2009). However, managers perceive that shrub colonization of abandoned *S. tenacissima* steppes is often absent or too slow and that this delay may compromise the delivery of ecosystem services and ecosystem stability. In this context, an increased understanding of the endogenous and exogenous factors controlling shrub colonization may therefore help to clarify the relationship between biotic/abiotic and structural/functional ecosystem components (sensu Turnbull et al., 2008), and prioritize restoration efforts in semiarid steppes.

The aim of the present study is to relate long-term shrub dynamics with biotic and abiotic ecosystem attributes. We used a set of aerial photographs (1956, 1978, 1985, 1998 and 2009) and field data to relate shrub patch dynamics to biotic, climatic, topographic and geomorphological properties of 27 abandoned steppes in SE Iberian Peninsula. The use of aerial photographs has several advantages over other methodological approaches (Morgan et al., 2010) and has been widely used in studies of shrub colonization (Hellesen and Levin, 2013; Hudak

and Wessman, 1998; Laliberté et al., 2004; Ward et al., 2014). We hypothesized that the effect of species identity and climate may be more influential in shaping long-term processes of shrub colonization than other factors related to the physical context of each abandoned steppe. Specifically, we expect that the rate and intensity of shrub colonization may depend on the identity of the colonizing species, and also on how species respond to climate in particular physical contexts characterized by topographic and geomorphological features. Describing shrub dynamics in abandoned steppes can be of great help to identify species with high and low ability to colonize under present and future climatic conditions. Furthermore, disentangling how long-term shrub dynamics are mediated by biotic and abiotic ecosystem attributes is crucial to prioritize management interventions because it provides evidences of suitable and unsuitable areas for establishment.

2. Material and Methods

2.1 Study sites

We selected fifteen catchments covered by *Stipa tenacissima* L. steppes in a semiarid area in Alicante, SE Spain (38º 20' 50''N, 0º 29' 29'' W), where winters are mild and summer drought is intense. Mean annual precipitation ranges between 282 and 525 mm, and mean annual air temperature between 15ºC and 18ºC (Ninyerola et al., 2005). Most soils are Lithic Calciorthid (Amat, 2015). Catchment surface area ranged between 3-11 ha, and were located within a 60-km NE-SW transect. Each catchment was divided into 3-6 environmental units (EU) on the basis of their aspect, topography, plant cover and previous land use. We identified 27 EUs in total based on the analysis of aerial photographs and field validation during a survey conducted in 2009.

2.2 Biotic and abiotic attributes of the environmental units

We measured biotic, climatic, topographical and geomorphological attributes in one to three 15 x 21m plots set in each EU, depending on its surface area. In each plot we established two 21m transects, 8 m apart, parallel to the maximum slope. In total we sampled 106 transects. In each

transect, we quantified plant cover and rock cover by visual estimation in 14 consecutive 1.5 x 1.5 m quadrats. Total plant cover was estimated as the sum of all species present in the transect. Rock cover was estimated as the sum of the cover of unconsolidated rocks as well as the cover of bedrock that appeared at the surface of the ground.

In each 21m transect, we estimated indicators of ecosystem function, such as patch area (hereafter resource sink area), and the average "inter-patch" length, following Landscape Functional Analysis approach (LFA; Tongway and Hindley, 2004). In this method, a patch is every long-lived feature that acts as a sink for resources by obstructing or diverting water flow and thus collecting and filtering water, nutrients, seeds (e.g., grass tussocks, large rock fragments, branches and litter). Accordingly, "inter-patches" are gaps between resource sinks, as bare soil, gravels, and plants whose structure is unable to retain resources (hereafter fetches).

Additionally, we georeferenced all shrub patches present in each EU in 2009 to calculate shrub patch density. Shrub patch density was calculated in each EU by dividing the total number of shrub patches by EU surface area. Field measurements of shrub patch density were used to assess the accuracy of aerial photograph interpretations (see below). We recorded species composition and the presence of dominant species (6 species in total) in 30 randomly selected patches (450 patches in total). We considered as dominant species those shrubs that form clearly defined patches, because of their large size and their ability to create new microhabitats. The six dominant species were *Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Juniperus oxycedrus* L., *Ephedra fragilis* Desf. and *Osyris lanceolata* Hochst. & Steud (Amat, 2015). Species richness was recorded as the total number of species per EU. We measured soil depth by inserting a 1-cm diameter iron rod into the soil and recording the maximum depth attained. Average soil depth under a shrub patch was estimated by measuring 6-10 points beneath their canopy. Average soil depth in each EU was estimated from the soil depth measured in 30 randomly chosen locations within each catchment.

We recorded elevation (m a.s.l.), slope (%) and predominant aspect of each EU using digital elevation models. To avoid confusion with the circular nature of aspect, we calculated the cosine of its value (hereafter northness). This transformation generates values between 1 (if the aspect is northwards) and -1 (if the aspect is southwards). We employed published records to estimate local mean annual precipitation (mm) from 1945 to 2009 (MOPREDAS database, González-Hidalgo et al., 2011), and mean annual air temperature (ºC) (Ninyerola et al., 2005). From the mean annual precipitation database, we calculated the standardize precipitation index (SPI) for each EU and year. The SPI has been widely used to estimate drought intensity, and is computed as the number of standard deviations that the average precipitation over a given period of time deviates from the long-term mean (Vicente-Serrano, 2006). The main properties of all EU's, and a schematic view of the sampling design are summarized as supplementary information (Table A1, Fig. A1).

2.3 Aerial photography interpretation

Aerial photos were obtained from public and commercial flights launched in 1956, 1978, 1985, 1998 and 2009 (Table 1). Digitized images of 1998 and 2009 were acquired, georeferenced and orthorectified. Photos from 1956, 1978 and 1985 were digitized by scanning on an A3 flatbed scanner (HP Deskscan, HP Co., Palo Alto, USA) at 1200 dpi, using an 8-bit grey-scale. Images were geometrically corrected, resampled to a common spatial resolution (1 m) and registered to the UTM projection by performing and image-to-image registration on 40 points from 2009 images (Fig. A2).

A texture layer was created from each image to enhance the difference between dark shrub canopies and the surrounding bright soil and herbaceous vegetation (Asner et al., 2003). Specifically, texture analysis consisted of passing a 3 x 3 pixel window computing the mean, variance and range within the kernel. Visual interpretation of generated images was performed to mark the presence of patches. Our sample unit was a shrub patch, defined as a woody plant canopy which represents and individual or a cluster of individuals with overlapping canopies

sensu (sensu Browning et al., 2008). In each texture layer, the same author (VR) marked the location of each shrub patch within the EU, to minimize observer bias. We related field measurements of shrub patch density and estimations based on aerial photographs to assess the accuracy of our approach. In addition, we estimated the detection probability of shrub patches using the double observer approach. This approach is commonly used in point count studies to provide estimates of population size and detection probability (Williams et al., 2002). It requires two independent counts of the same subjects to estimate detection probability. We used shrub patches georeferenced in 2009 field survey as a benchmark. Detection probability of the visual interpretation of aerial photographs (p) can be computed as $p = m_2/n_1$. Where m_2 is the number of shrub patches detected in both surveys (aerial photographs and field observations) and n_1 is the number of shrub patches identified on aerial photographs. We used ArcGIS v.9.3 (Environmental Science Research Institute, Redlands, California, USA) to process, quantify and classify information obtained from images.

2.4 Data analysis

The relationship between patch species composition and biotic and abiotic attributes was explored using redundancy analysis (RDA). The response variables were the abundance of the dominant shrub species recorded in the field survey, and explanatory variables were the biotic, climatic, topographical and geomorphological attributes. The significance of total canonical variation and individual eigenvalues were tested with permutation methods.

Shrub patch dynamics was analyzed in different ways. Firstly, we used generalized linear mixed models to assess the relationship between temporal dynamics of shrub patch density (i.e. dependent variable) and biotic, climatic, topographical and geomorphological attributes (i.e. independent variables). Moreover, we included year in the model as ann independent variable to test for differences in shrub patch density between time steps. We included precipitation and SPI as the averaged value in the decade prior to each aerial photograph. We did not include temperature because of the lack of complete data. We included site scores of the first two axes

206 of the RDA (hereafter RDA1 and RDA2) in the biotic matrix to account for the effect of species
207 composition on shrub patch density. Site scores are the coordinates of the sites expressed in the
208 space generated by the species abundance matrix, without the influence of independent
209 variables included in the RDA (Borcard et al., 2011). To account for differences in surface area
210 between EUs, these values were included in the model as an offset (Zuur et al., 2009). We
211 included the random effect of catchment and year in a varying intercept and slope model, to
212 account for repeated measures of patch density over time (Bates, 2010). To account for the
213 differences in image quality between aerial photographs (Table 1), we categorized scale as
214 small-scale (1/35.000 and 1/40.000), mid-scale (1/18.000) and large-scale (1/5.000) and
215 included as a random effect in the model.
216
217 Secondly, the rate of shrub colonization was analyzed by fitting non-linear functions to shrub
218 patch density increment ratios. Shrub patch density increment ratios (PD_r) (adapted from Gale
219 and Grigal, 1987) at each time step were calculated as: $PD_r = (t_i - t_o)/(t_f - t_o)$, where t_o is shrub
220 patch density in 1956, t_f is shrub patch density in 2009, and t_i is shrub patch density at
221 successive time steps (i = 1956, 1978, 1985, 1998, 2009). A set of non-linear models (i.e.
222 monomolecular, logistic and exponential) was fitted to the data to model the relationships
223 between PD_r values against time. In each site, we selected the function showing the best fit
224 based on the coefficient of determination to observational data (see Table A2 for a summary of
225 these analysis). Then, we solved each equation at $PD_r(t)= 0.5$ to estimate the time needed to
226 reach a 50% change in PD_r (t50; sensu Gale and Grigal, 1987). Thirdly, we calculated the total
227 change in shrub patch density in each EU from 1956 to 2009 (hereafter density change).
228
229 Linear mixed models containing t_{50}, density change and detection probability as dependent
230 variables and biotic, climatic and physical attributes were fit to the data, including catchment as
231 a random effect. We included RDA1 and RDA2 in the model to test the effect of species
232 identity, and initial patch density to test density-dependent effects. We could not include SPI
233 values in these models because its mean is zero when considering the whole precipitation time

234 series. Alternatively, we categorized each SPI values per year according to the National Drought
235 Mitigation Center of the USA (http://droughtmonitor.unl.edu) as: 0 ($+0.5 \leq SPI \geq -0.5$); −1
236 ($-0.5 < SPI > -0.8$); and -2 ($-0.8 \leq SPI > -1.3$). We only included the first three categories of
237 this classification scheme because our database did not contain values of SPI < -1.3. We
238 included the mean values of the new categorization per catchment in these models.
239 Additionally, we related averaged SPI values between two consecutive aerial photographs to
240 mean t_{50} values per catchment, to test if t_{50} values per catchment corresponded to periods of
241 higher water availability.
242
243 To evaluate which predictor variables contributed consistently across each model per response
244 variable (shrub patch density, t_{50}, density change and detection probability) we followed a
245 model averaging approach following Grueber *et al.*, (2011). For this, regression coefficients of
246 each explanatory variable were averaged across all competing models where ΔAICc < 2. For
247 each competing model, Akaike Information Criterion weight (AICc-wi), which represents the
248 likelihood of a given model relative to all other models, was generated. An importance value of
249 each explanatory variable was calculated by adding the AICc-wi values of the competing
250 models in which the predictor was present. Importance values vary between zero (low
251 importance) and one (high importance). Competing models were based on the combination of
252 explanatory variables whose variance inflation factor was below four, to avoid collinearity. All
253 analyses were carried out with R v3.0.1 (R Development Core Team, 2013). We employed
254 *vegan* (RDA), *SPEI* (SPI), *minpack.lm* (non-lineal fitting), *lme4* (GLMM), and *MuMIn*
255 (multimodel inference) packages.
256
257 **3. Results**
258 **3.1 Association of shrub patch species with biotic and abiotic attributes**
259 Redundancy analysis showed that 55% of the variance in species abundance was explained by
260 northness, soil depth, patch area, temperature and precipitation (Table 2). The first two
261 canonical axes explained 86% of the total variance, and were statistically significant (P = 0.005

for both axes after 999 permutations). Temperature and precipitation played an important role in EU dispersion along the first axis (Fig. 1). *Osyris lanceolata* abundance was positively correlated with precipitation, soil depth and northness. In contrast, the abundance of *Rhamnus lyciodes* and *Ephedra fragilis* were positively correlated with temperature. Resource sink area was weakly correlated with *Quercus coccifera* abundance. The position of other species in the space defined by the two axes was intermediate.

3.2 Detection probability of shrub patches

The mean value of detection probability across EUs was 0.73 (± 0.03). Rock cover, plant cover and fetch length showed positive model coefficient estimates of detection probability (Table 3). However, coefficient estimates of the three attributes were not different from zero. Estimated shrub patch density from aerial photographs was positively and linearly related to shrub patch density measured in the field ($P < 0.001$, $r^2 = 0.77$) (Fig. A3).

3.3 Influence of biotic and abiotic attributes on changes in shrub patch density and colonization rate

Aerial photograph interpretation showed that shrub patch density increased from 24 ± 3.2 to 67 ± 7.4 patches ha^{-1} (average ± SE) over the 53-years period. Shrub patch density increased significantly in each time step as compared to the reference value in 1956 (Table 3). The best set of predictors for shrub patch density included year, precipitation, northness, rock cover, resource sink area and plant cover in 2009 (Table 3). We observed a negative association between shrub patch density and precipitation, northness, rock cover, and resource sink area. Plant cover was positively associated with shrub patch density.

Three contrasting patterns of change were observed when increases in shrub patch density were standardized (Fig. 2, Table A2). In 18 EUs, they followed a logistic growth curve, whereas in other EUs, the pattern was better explained by a monomolecular curve (4 EUs) or an exponential curve (5 EUs). The coefficients of all equations were strongly significant, and all

curves showed good fit (Table A2). The average time to achieve 50% of the maximum shrub patch density (t_{50}) was 10.3 ± 1.4, 28.2 ± 1.2, and 44.4 ± 0.1 years (± SE) in EUs following monomolecular, logistic and exponential increases, respectively. The abundance of *Q. coccifera* was negatively related to t_{50} indicative of early recruitment patterns (Fig. 3). By contrast, *O. lanceolata* was positively related to t_{50}, indicative of late recruitment. Mean annual precipitation, SPI, and species composition were important predictors of t_{50} (Table 3). All three explanatory variables were positively associated with $t_{50.}$ For a given combination of precipitation and species identity, t_{50} was lower (i.e., colonization faster) in EUs where average SPI values were lower. The change in the sign of the relationship between SPI and t_{50} along the studied period further confirmed the control of water availability on colonization rate (Fig. 4). SPI and t_{50} showed a negative relationship before 1978. Conversely, between 1998-2009, this relation was positive (Fig. 4). Rock cover, plant cover, resource sink area and fetch length were positively related to t_{50}. Temperature showed a weak negative effect on t_{50}. The intensity of colonization of each EU, defined as the absolute density change in the entire study period, was negatively influenced by resource sink area and initial shrub patch density, and positively affected by plant cover, SPI, and temperature (Table 3). Although composition was not a significant predictor of density change, we observed that the abundance of *Q. coccifera* was negatively associated with density change, whereas *E. fragilis* and *R. lyciodes* were positively related (Fig. 3).

4. Discussion

Our results conformed to the expectation that species identity and climate are important drivers of shrub colonization. Previous studies on temporal patterns of shrub colonization have mostly focused on the role of site conditions (Browning et al., 2008; Davies et al., 2010; Levick and Rogers, 2011), fire (Malkisnon et al., 2011) and grazing (Roques et al., 2001). We observed that aspect and rock cover were significant predictors of shrub patch density. However, our results showed that the biotic characteristics of the colonizing species coupled with changes in climatic conditions were more influential than topographic and geomorphological features as

rock cover and aspect. Indeed, we found that shrub patch colonization in these semiarid steppes was very sensitive to climatic conditions. We observed that colonization was limited along periods of low water availability (low SPI). Thus, catchments with low t_{50}, showed high values of SPI early after abandonment, and low values of SPI at the end of the study period. We observed the opposite pattern in catchments with high t_{50} (Fig. 4). In addition, we found that mean annual precipitation and mean annual temperature appeared in most models of patch dynamics. These results are in accordance with the major limit that water availability imposes on the functioning and persistence of Mediterranean vegetation (Peñuelas et al., 2001), and suggest that the topographic and geomorphological factors may only affect shrub colonization once climatic filters are overcome.

4.1 Species identity and non-linear patterns of shrub colonization

Results from experimental plantations have shown that species identity can play a major role in the success of restoration efforts of semiarid areas (Padilla et al., 2009b). Our results accord with these findings and highlight the importance of species identity in the processes of shrub colonization. Differences in colonization rate may emerge soon after the end of disturbance. The way plants overcome critical bottlenecks, such as summer drought during the first stages of succession, may shape community assemblage in semiarid systems (Schulze et al., 1996). In *S. tenacissima* steppes, plant traits related to seed phenology, dormancy and dispersal range, vulnerability to predation, and rooting capacity may generate different sequences of shrub colonization (Barberá et al., 2006; García-Fayos and Verdu, 1998; Mendoza-Aguilar et al., 2014).

We observed that EUs with different shrub species showed different colonizing trajectories. On one hand, the positive association between t_{50} and RDA2, and the negative relation between the latter and the abundance of *Q. coccifera*, suggest that in EUs where this species was abundant, colonization was fast and maximum patch density was achieved in few years. The negative association between *Q. coccifera* and t_{50} and density change supports this finding (Fig. 3). Two

346 alternative processes may explain this pattern. On the one hand, the rapid increase in patch
347 density may reflect the ability of *Q. coccifera* and other patch forming species to resprout. In
348 patch-forming species, resprouters usually grow faster than mature plants and seedlings (Castell
349 et al., 1994), which is in agreement with the fast colonization rates observed in some
350 catchments. On the other hand, the formation of new patches dominated by *Q. coccifera* may
351 also rely on successful acorn dispersal and the availability of safe sites (Eriksson and Ehrlén,
352 1992). These safe sites may become saturated early, when patch density reaches an asymptote
353 (Browning et al., 2008). However, the slow growth rate of planted *Q. coccifera* seedlings
354 (Vilagrosa et al., 2014, 2003) suggests that seedling establishment was not the main process
355 behind the increase in *Q. coccifera* patches.
356
357 We found the opposite situation in other EUs, particularly where *E. fragilis* was abundant. In
358 those EUs, shrub patch density increased slowly after abandonment, and showed no signs of
359 stabilization after 54 years. Exponential colonization curves probably reflect the dominance of
360 seeding vs. resprouting strategies, and the presence of limiting factors for early establishment,
361 such as a lack of seeds and absence of suitable nurse species or safe-sites for dispersal
362 (Reisman-Berman et al., 2006). *Ephedra fragilis* withstands harsh environmental conditions,
363 although its ability to grow fast and root depth is less than those of other semiarid shrubs as
364 *Salsola oppositifolia* Desf., *Retama sphaerocarpa* (L.) Boiss. and *Olea europaea* L. (Padilla et
365 al., 2009a; Padilla and Pugnaire, 2007, 2009).
366
367 Finally, colonization in most EUs followed a logistic curve, which suggests a mixture of
368 seeding and resprouting strategies. Briggs *et al.*, (2002) reported similar responses when
369 analyzing encroachment in northeast Kansas grasslands, and found that maximum woody cover
370 was reached after 40 years. Interestingly, we did not find bimodal patch recruitment curves or
371 other curve types that would suggest consecutive phases of colonization.
372

As discussed above, early colonization may be favored by higher availability of seeds and buds and suitable environmental conditions. In contrast, the absolute change in patch density may be limited by other factors such as biotic interactions. The negative relationship between total density change and initial patch density suggests that as shrub patch density increased, intra- and inter-specific interference became increasingly intense. These results are in accordance with density-dependent processes observed in other semiarid environments, and may control ecosystem structure and dynamics (Skarpe, 1991; Wiegand et al., 2006).

4.2 Abiotic factors and shrub patch dynamics

In areas subjected to harsh environmental conditions, colonization started later, but total changes in shrub patch density were larger than in less demanding areas. This was corroborated by the negative association found between precipitation and shrub patch density. Climatic conditions will likely change in the next decades. Air temperature will increase and precipitation will decline and be concentrated in fewer events (IPCC, 2007). Considering the trends observed in our retrospective study, we hypothesize that the abundance of patches dominated by *E. fragilis* will increase at the expense of those dominated by *P. lentiscus*. In this line, according to field evidences and our own results, future climatic and disturbance regimes may have contrasting effects for the persistence of some patch-forming species leading to changes in the composition of species of the studied system (Delitti et al., 2005; Peñuelas et al., 2001).

Nevertheless, the consistent increase in patch density suggests that shrub recruitment was not impaired, and degraded steppes were capable of self-recovery (Maestre et al., 2007). Experimental planting of late-successional shrubs have shown that shrubs can establish in steppes with reduced capacity to capture and hold water, sediments and nutrients, i.e., reduced catchment functionality. Indeed, short-term seedling performance can be negatively related to catchment functionality (Maestre et al., 2006), which is consistent with the interference exerted by *S. tenacissima* tussocks on shrub establishment under severe drought (Maestre et al., 2001). The observed positive effect of plant cover on shrub colonization dynamics is consistent with an

interference effect of pre-existing vegetation on shrub establishment. Woody patches in *S. tenacissima* steppes, and particularly those dominated by species with dense canopies as *Q. coccifera*, facilitate the establishment of new individuals (Amat et al., 2015). Additionally to the observed positive effect of plant cover, the effect of resource sinks suggests that catchment functionality can also affect shrub colonization. Overall, our results suggest that the studied sites had not previously crossed a biotic resilience threshold (Cortina et al., 2012; Mayor et al., 2013; Whisenant, 1999).

4.3 Management implications

Our results have clear implications for the management of *S. tenacissima* steppes. On the one hand, shrub patch density ranged from 11 to 143 patches ha^{-1}, which is much lower than the density used in most plantation programs (Serrada, 2000). This observation should be taken into account when evaluating plantation success in semiarid steppes. On the other hand, the increase in shrub patch density in all EUs ranged from 0.1 to 2.0 new patches ha^{-1} $year^{-1}$; 75% of these were less than one patch ha^{-1} $year^{-1}$. As average shrub patch density was 67 patches ha^{-1}, it may take more than a century to attain these values in most EUs. Thus, planting patch-forming species may help to increase the rate of patch formation. This is particularly true for patches dominated by 'slow' species or species located at the upper end of the RDA2 axis (e.g., *E. fragilis* vs. *Q. coccifera*, Fig. A4). Finally, the non-linear increase in patch density and its relationship with climatic conditions should be taken into account, as it could help identify suitable periods for planting, and for optimizing watering and moisture conservation programs.

4.4 Conclusions

We conclude that shrub patches have colonized and expanded in abandoned *S. tenacissima* steppes in the southeastern Iberian Peninsula. This process is likely to continue in some areas, but not in those where shrub patch density has remained stable over the last decade. Colonization trajectories are largely controlled by the identity of patch-forming community and climatic conditions, particularly precipitation. Species-specific responses to climatic conditions

should be taken into account when selecting new areas for planting in restoration programs. Given the sensitivity of patch-forming species to climatic conditions, new challenges for the management of *S. tenacissima* steppes will likely emerge under the influence of climate change.

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References

Alados, C.L., Pueyo, Y., Barrantes, O., Escós, J., Giner, L., Robles, A.B., 2004. Variations in landscape patterns and vegetation cover between 1957 and 1994 in a semiarid Mediterranean ecosystem. Landsc. Ecol. 19, 543–559.

Amat, B., 2015. Dynamics of woody vegetation patches in semiarid ecosystems in the southeast of the Iberian Peninsula. University of Alicante, Spain.

Amat, B., Cortina, J., Zubcoff, J.J., 2015. Community attributes determine facilitation potential in a semi-arid steppe. Perspect. Plant Ecol. Evol. Syst. 17, 24–33.

Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. Glob. Change Biol. 9, 316–335.

Barberá, G.G., Navarro-Cano, J.A., Castillo, V.M., 2006. Seedling recruitment in a semi-arid steppe: The role of microsite and post-dispersal seed predation. J. Arid Environ. 67, 701–714.

Bartolomé, J., López, Z.G., Broncano, M.J., Plaixats, J., 2005. Grassland colonization by *Erica scoparia* (L.) in the Montseny Biosphere Reserve (Spain) after land-use changes. Agric. Ecosyst. Environ. 111, 253–260.

Bates, D., 2010. lme4: Mixed-effects modeling with R. Springer, Heidelberg, Germany.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer.

Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the Rate, Mechanisms, and Consequences of the Conversion of Tallgrass Prairie to Juniperus virginiana Forest. Ecosystems 5, 578–586.

Browning, D.M., Archer, S.R., Asner, G.P., McClaran, M.P., Wessman, C.A., 2008. Woody plants in grasslands: Post-encroachment stand dynamics. Ecol. Appl. 18, 928–944.

Castell, C., Terradas, J., Tenhunen, J., 1994. Water relations, gas exchange, and growth of resprouts and mature plant shoots of *Arbutus unedo* L. and *Quercus ilex* L. Oecologia 98, 201–211.

Cortina, J., Amat, B., Castillo, V., Fuentes, D., Maestre, F.T., Padilla, F.M., Rojo, L., 2011. The restoration of vegetation cover in the semi-arid Iberian southeast. J. Arid Environ. 75, 1377–1384.

Cortina, J., Ruíz-Mirazo, J., Amat, B., Amghar, F., Bautista, S., Chirino, E., Derak, M., Fuentes, D., Maestre, F.T., Valdecantos, A., Vilagrosa, A., 2012. Les bases de la restauration écologique des steppes d´alfa, VI. ed. UICN, Gland, Suisse et Malaga, Espagne.

Davies, K.W., Petersen, S.L., Johnson, D.D., Davis, D.B., Madsen, M.D., Zvirzdin, D.L., Bates, J.D., 2010. Estimating Juniper cover from National Agriculture Imagery Program (NAIP) imagery and evaluating relationships between potential cover and environmental variables. Rangel. Ecol. Manag. 63, 630–637.

Delitti, W., Ferran, A., Trabaud, L., Vallejo, V.R., 2005. Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia Region (Spain): I. plant composition and productivity. Plant Ecol. 177, 57–70.

D'Odorico, P., Okin, G.S., Bestelmeyer, B.T., 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology 5, 520–530.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14, 709–722.

Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91, 360–364.

Gale, M.R., Grigal, D.F., 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. For. Res. 17, 829–834.

García-Fayos, P., Verdu, M., 1998. Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. Acta Oecologica 19, 357–366.

González-Hidalgo, J.C., Brunetti, M., de Luis, M., 2011. A new tool for monthly precipitation analysis in Spain: MOPREDAS database (monthly precipitation trends December 1945–November 2005). Int. J. Climatol. 31, 715–731.

Gross, N., Boerger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., Garcia-Gomez, M., Valencia-Gomez, E., Maestre, F.T., 2013. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. J. Ecol. 101, 637–649.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711.

Hellesen, T., Levin, G., 2013. Methodology to estimate loss of semi-natural grasslands due to shrub encroachment in Denmark from 1965 to 2010–a sample-based study using dot grids on aerial photographs. J. Land Use Sci. 0, 1–18.

Hodgkinson, K.C., 1998. Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oecologia 115, 64–72.Hudak, A.T., Wessman, C.A., 1998. Textural analysis of historical aerial photography to characterize woody plant encroachment in South African savanna. Remote Sens. Environ. 66, 317–330.

Iannone, B.V., Zellner, M.L., Wise, D.H., 2014. Modeling the impacts of life-history traits, canopy gaps, and establishment location on woodland shrub invasions. Ecol. Appl. 24, 467–483.

IPCC, 2007. Climate change 2007: synthesis report, in: Pachauri, R.K., Reisinger, A., Core Writing Team (Eds.), Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, p. 104.

Laliberté, A.S., Rango, A., Havstad, K.M., Paris, J.F., Beck, R.F., McNeely, R., Gonzalez, A.L., 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. Remote Sens. Environ. 93, 198–210.

Levick, S.R., Rogers, K.H., 2011. Context-dependent vegetation dynamics in an African savanna. Landsc. Ecol. 26, 515–528.
Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecol. Appl. 11, 1641–1655.
Maestre, F.T., Bowker, M., Puche, D., Hinojosa, M., Martínez, I., García-Palacios, P., Castillo, A., Soliveres, S., Luzuriaga, A., Sánchez, A., Carreira, J., Gallardo, A., Escudero, A., 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. Ecol. Lett. 12, 930–941.
Maestre, F.T., Ramírez, D.A., Cortina, J., 2007. Ecología del esparto (*Stipa tenacissima* L.) y los espartales de la Península Ibérica. Rev. Ecosistemas 16.
Maestre, F., Valladares, F., Reynolds, J., 2006. The stress-gradient hypothesis does not fit all relationships between plant-plant interactions and abiotic stress: further insights from arid environments. J. Ecol. 94, 17–22.
Malkisnon, D., Wittenberg, L., Beeri, O., Barzilai, R., 2011. Effects of repeated fires on the structure, composition, and dynamics of Mediterranean maquis: Short- and long-term perspectives. Ecosystems 14, 478–488.
Mayor, A.G., Kéfi, S., Bautista, S., Rodríguez, F., Cartení, F., Rietkerk, M., 2013. Feedbacks between vegetation pattern and resource loss dramatically decrease ecosystem resilience and restoration potential in a simple dryland model. Landsc. Ecol. 28, 931–942.
Mendoza-Aguilar, D.O., Cortina, J., Pando-Moreno, M., 2014. Biological soil crust influence on germination and rooting of two key species in a *Stipa tenacissima* steppe. Plant Soil 375, 267–274.
Morgan, J.L., Gergel, S.E., Coops, N.C., 2010. Aerial photography: A rapidly evolving tool for ecological management. BioScience 60, 47–59.
Munson, S.M., Webb, R.H., Housman, D.C., Veblen, K.E., Nussear, K.E., Beever, E.A., Hartney, K.B., Miriti, M.N., Phillips, S.L., Fulton, R.E., Tallent, N.G., 2015. Long-term plant responses to climate are moderated by biophysical attributes in a North American desert. J. Ecol. 103, 657–668.
Ninyerola, M., Joure, J.M., Pons Fernández, X., 2005. Atlas climático digital de la Península Ibérica: metodología y aplicaciones en bioclimatología y geobotánica. Bellaterra : Centre de Recerca Ecológica i Aplicacions Forestals, Spain.
Padilla, F.M., Miranda, J.D., Jorquera, M.J., Pugnaire, F.I., 2009a. Variability in amount and frequency of water supply affects roots but not growth of arid shrubs. Plant Ecol. 204, 261–270.
Padilla, F.M., Ortega, R., Sánchez, J., Pugnaire, F.I., 2009b. Rethinking species selection for restoration of arid shrublands. Basic Appl. Ecol. 10, 640–647.
Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Funct. Ecol. 21, 489–495.
Padilla, F., Pugnaire, F., 2009. Species Identity and Water Availability Determine Establishment Success Under the Canopy of Retama sphaerocarpa Shrubs in a Dry Environment. Restor. Ecol. 17, 900–907.
Peñuelas, J., Lloret, F., Montoya, R., 2001. Severe drought effects on Mediterranean woody flora in Spain. For. Sci. 47, 214–218.
Peters, D.P.C., Bestelmeyer, B.T., Herrick, J.E., Fredrickson, E.L., Monger, H.C., Havstad, K.M., 2006. Disentangling complex landscapes: New insights into arid and semiarid system dynamics. Bioscience 56, 491–501.
Pueyo, Y., Kefi, S., Diaz-Sierra, R., Alados, C.L., Rietkerk, M., 2010. The role of reproductive plant traits and biotic interactions in the dynamics of semi-arid plant communities. Theor. Popul. Biol. 78, 289–297.
R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reisman-Berman, O., Kadmon, R., Shachak, M., 2006. Spatio-temporal scales of dispersal limitation in the recolonization of a semi-arid mediterranean old-field. Ecography 29, 418–426.

576 Roques, K.G., O'Connor, T.G., Watkinson, A.R., 2001. Dynamics of shrub encroachment in an
577 African savanna: relative influences of fire, herbivory, rainfall and density dependence.
578 J. Appl. Ecol. 38, 268–280.
579 Ruppert, J.C., Harmoney, K., Henkin, Z., Snyman, H.A., Sternberg, M., Willms, W., Linstädter,
580 A., 2015. Quantifying drylands' drought resistance and recovery: the importance of
581 drought intensity, dominant life history and grazing regime. Glob. Change Biol. 21,
582 1258–1270.
583 Schulze, E.-D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J.,
584 Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J.R., 1996. Rooting depth, water
585 availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia 108,
586 503–511.
587 Serrada, R., 2000. Apuntes de repoblaciones forestales. FUCOVASA, Madrid.
588 Skarpe, C., 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. J. Veg.
589 Sci. 2, 565–572.
590 Tongway, D., Hindley, N., 2004. Landscape function analysis manual: procedures for
591 monitoring and assessing landscapes with special reference to minesites and
592 rangelands., in: CSIRO Sustainable Ecosystems. Camberra, Australia.
593 Turnbull, L., Wainwright, J., Brazier, R.E., 2008. A conceptual framework for understanding
594 semi-arid land degradation: ecohydrological interactions across multiple-space and time
595 scales. Ecohydrology 1, 23–34.
596 van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western
597 North American grasslands. J. Environ. Manage. 90, 2931–2942.
598 Vicente-Serrano, S.M., 2006. Evaluating the impact of drought using remote sensing in a
599 Mediterranean, semi-arid region. Nat. Hazards 40, 173–208.
600 Vilagrosa, A., Bellot, J., Vallejo, V.R., Gil-Pelegrín, E., 2003. Cavitation, stomatal conductance,
601 and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an
602 intense drought. J. Exp. Bot. 54, 2015–2024. doi:10.1093/jxb/erg221
603 Vilagrosa, A., Hernández, E.I., Luis, V.C., Cochard, H., Pausas, J.G., 2014. Physiological
604 differences explain the co-existence of different regeneration strategies in
605 Mediterranean ecosystems. New Phytol. 201, 1277–1288.
606 Ward, D., Hoffman, M.T., Collocott, S.J., 2014. A century of woody plant encroachment in the
607 dry Kimberley savanna of South Africa. Afr. J. Range Forage Sci. 31, 107–121.
608 Whisenant, S., 1999. Repairing damaged wildlands: A process-orientated, landscape-scale
609 approach. Cambridge University Press.
610 Wiegand, K., Saitz, D., Ward, D., 2006. A patch-dynamics approach to savanna dynamics and
611 woody plant encroachment - Insights from a savanna. Perspect. Plant Ecol. Evol. Syst.
612 7, 229–242.
613 Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and management of animal
614 populations: Modeling, estimation, and decision making. Academic Press.
615 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models
616 and extensions in ecology with R. Springer, New York.

Table 1. Main features of the different sets of aerial photographs included in the time series analysis.

Year	Source	Colour	Scale	Pixel size (m)
1956	American Flight Serie B	Grey scale	1/35.000	0.5
1978	Interministerial Flight	Grey scale	1/18.000	0.5
1985	Interministerial Flight	Grey scale	1/18.000	0.5
1998	Olysat (Sig Oleicola)	Grey scale	1/40.000	1
2009	CNIG	Color (RGB)	1/5000	0.5

Table 2. Final set of significant descriptors included in the RDA analysis to describe the relationship between biotic and abiotic attributes and species composition in shrub patches.

	df	F	*P-value*
Aspect (northness)	1	2.6	0.035
Soil depth	1	4.3	0.001
Patch area	1	2.3	0.056
Mean annual air temperature	1	10.9	< 0.001
Mean annual precipitation	1	5.2	< 0.001

Table 3. Coefficient estimates, adjusted standard errors (SE) and confidence intervals (95%) describing shrub colonization after model averaging of GLMMs. Estimates represent standardize values and, therefore, they are in a comparable scale. Shrub patch density in 1956 is the reference level for the factor year in the shrub patch density model. The relative importance of predictor variables was calculated as the sum of AICc-wi values of the competing models in which the predictor was present.

		Estimate	SE	Conf. Interval (5 - 95%)	Importance
Patch density	Intercept	17.10	5.4	8.24, 25.95	
	Resource sink area	-4.47	1.91	-7.63, -1.31	1.00
	Year 1978	16.06	3.67	9.97, 22.16	1.00
	Year 1985	17.77	4.6	10.13, 25.42	1.00
	Year 1998	32.08	5.5	23.61, 42.01	1.00
	Year 2009	43.98	6.65	32.96, 54.99	1.00
	Precipitation	-5.41	2.23	-9.11, -1.72	0.79
	Plant cover	3.14	1.28	1.02, 5.26	0.67
	Aspect (northness)	-2.74	1.19	-4.72, -0.76	0.42
	Rock cover	-2.68	1.14	-4.57, -0.79	0.33
t_{50}	Intercept	28.53	1.67	25.82, 31.25	
	Precipitation	5.27	2.02	1.98, 8.56	0.70
	RDA2	3.75	2.01	0.49, 7.02	0.60
	SPI	3.42	1.74	0.60, 6.24	0.44
	Rock cover	2.89	1.73	0.09, 5.69	0.36
	Plant cover	4.58	2.06	1.22, 7.93	0.27
	Resource sink area	3.17	1.82	0.22, 6.12	0.26
	Fetch length	3.2	1.95	0.05, 6.35	0.04
	Temperature	-3.54	1.75	-6.37, -0.69	0.03
Density change	Intercept	46.33	6.83	35.17, 57.48	
	Plant cover	15.21	3.22	9.99, 20.43	1.00
	SPI	14.8	4.71	7.13, 22.46	1.00
	Temperature	25.67	5.07	17.4, 33.94	1.00
	Resource sink area	-9.84	4.32	-16.88, -2.79	0.61
	Initial density	-0.48	0.23	-0.85, -0.10	0.28
Detection probability	Intercept	0.55	0.02	0.51, 0.59	
	Plant cover	0.02	0.01	-0.01, 0.04	0.24
	Rock cover	-0.01	0.01	-0.02, 0.01	0.18
	Fetch length	-0.01	0.01	-0.03, 0.01	0.18

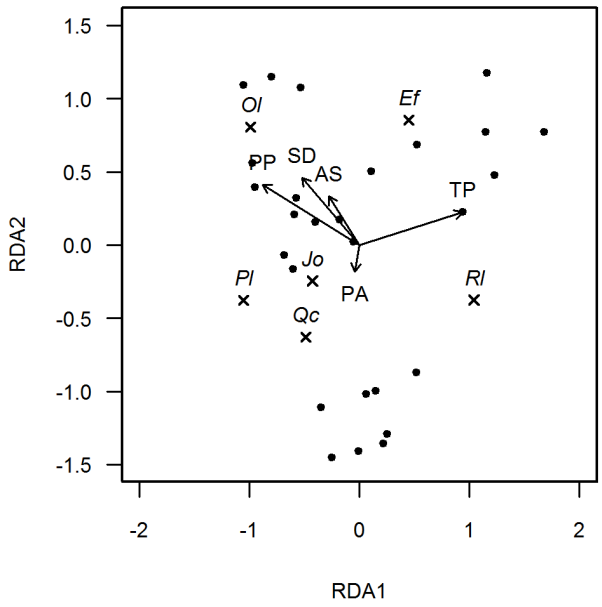


Figure 1. RDA triplot depicting the abundance of the dominant patch forming shrub species as a function of biotic [resource sink area (PA)] and abiotic [aspect as standardized as northness (AS), soil depth (SD), precipitation (PP) and temperature (TP)] ecosystem attributes. Circles and crosses represent environmental units and dominant patch forming species, respectively. Codes for species names are as follows: *Ephedra fragilis* (Ef), *Rhamnus lycioides* (Rl), *Quercus coccifera* (Qc), *Juniperus oxycedrus* (Jo), *Pistacia lentiscus* (Pl) and *Osyris lanceolata* (Ol).

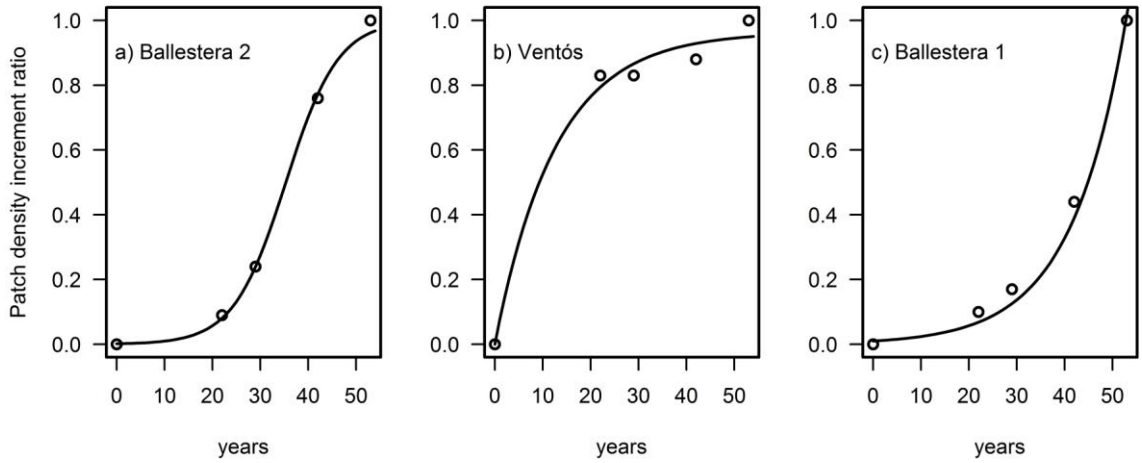
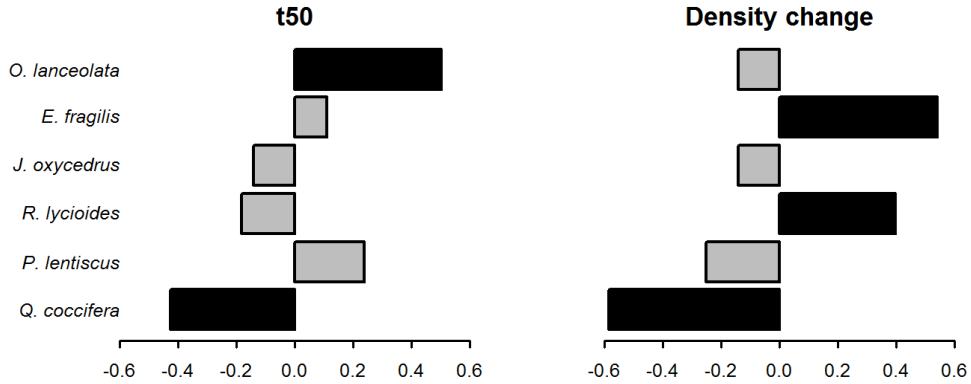


Figure 2. Examples of non-linear curve fitting of patch density increment ratio as a function of time of three EUs. The three non-linear response found were logistic a), monomolecular b) and exponential c).



650

651

652 Figure 3. Spearman rank correlations between abundance of dominant species and variables of

653 shrub colonization dynamics (t_{50} and density change). Dark bars depict significant associations

654 at $P < 0.05$.

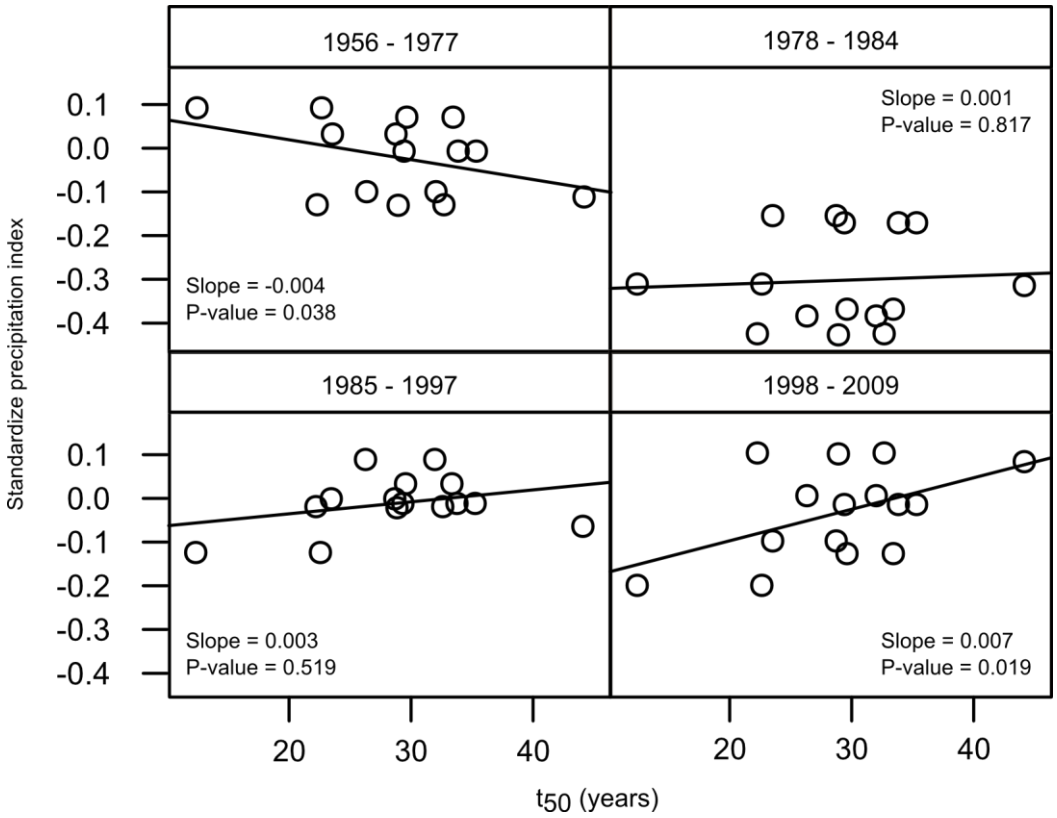


Figure 4. Relation between average values of SPI and t_{50} per catchment at time steps defined between two consecutive aerial photographs.